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Multi-decadal surveys in a Mediterranean forest reserve – do succession and isolation drive moth species richness?

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Abstract

Isolated fragments of semi-natural habitats are often embedded in a landscape matrix that is hostile to organisms of conservation concern. Such habitat islands are prone to changes in their biota over time. For insects, few studies on long-term trends in species richness within conservation areas are available, mainly due to the lack of historical data. We here use moths in the coastal pine wood reserve Pineta san Vitale (Ravenna, NE Italy) to assess how local fauna has changed over the last 85 years. This reserve has experienced massive changes in vegetation structure due to secondary succession. We compared historical collections (1933–1976: 107 species; and 1977–1996: 157 species) with our own samples (1997–2002: 174 species; and 2011+2012: 187 species). Over the last 85 years, the proportion of habitat generalists in relation to all recorded moth species increased from 20 to 33%. The fractions of woodland and open habitat species concomitantly decreased by 10 percentage points, respectively. Amongst woodland and habitat generalist species, gains outnumbered losses. In contrast, 18 species of open habitats and 10 reed species were lost over the decades. We attribute these changes to vegetation succession and to the isolation of the reserve. Generalist species are presumably better able to pass through anthropogenically exploited landscapes and colonise isolated habitat fragments than habitat specialists.

Keywords

Anthropogenic influence, biodiversity, conservation biology, generalists, habitat specialists, Italy, Lepidoptera, long-term changes, moth diversity

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Introduction

Mediterranean coastal pine forests are vulnerable and rare ecosystems. They provide habitat for many species, but have experienced massive contractions over centuries and are nowadays strongly at risk through anthropogenic land-use intensification (Gasparella et al. 2017). Only few coastal pine forests have persisted on the Italian Peninsula. Some of them have been awarded high legal conservation status (Gasparella et al. 2017), but the current status of their biodiversity is often imperfectly known (Scarascia-Mugnozza et al. 2000). In general, isolated nature reserves, embedded in a landscape matrix dominated by intense human land-use, run the risk of losing over time those organisms for which they had been established (Mora and Sale 2011). Even for large-sized conservation areas, such detrimental trajectories have been documented from a range of biomes (Gauthier et al. 2015, Hautier et al. 2015, Uhl et al. 2016). Some species may persist for decades in conservation areas, but eventually get lost over time, be it due to ecosystem degradation or just attributable to stochasticity. This notion has led to the concept of an extinction debt and, only in the long term, can it be evaluated whether organisms are really safe in the reserves that have been set aside for their conservation (Carroll et al. 2004, Halley et al. 2016). Especially in areas where anthropogenic influence has been severe over decades, long term studies are of great interest because they can mirror changes in an ecosystem best and shed light on the steady erosion of biodiversity (Habel et al. 2016).

To understand long-term changes of the insect fauna in an isolated nature reserve, we investigated moth communities in Pineta san Vitale (hereafter PsV). Nowadays protected as a Natura 2000 site (Montanari 2010) and listed in the Convention of Ramsar (Ramsar Convention Secretariat 2013) as "wetland of international importance", the coastal pine forest PsV, since the year 1988, forms part of the Parco Regionale del Delta del Po which is also covered under the EU life programme (http://ec.europa.eu). Therefore it is of high interest which long term changes might have taken place in this reserve.

Originally PsV is believed to have been covered by dune vegetation that later changed to a humid forest. Around the 12th century, Italian stone pine trees (*Pinus pinea*) were planted for wood and pine nut production. Timber extraction and commercial pine nut harvest were abandoned in 1988 when the Parco Regionale del Delta del Po was established (Enrica Burioli, pers. communication). In general, Italian coastal areas with wooded dune habitats show strong signs of vegetation succession during the past decades. In particular, the grassland fractions in these areas have prominently declined since the 1960s (Prisco et al. 2016). Comparisons of old photographs with the current vegetation status also indicate that, in PsV, shrub and tree cover has massively increased at the expense of grassland that historically provided a habitat for numerous non-forest species (Fig. 1).

Apart from succession, there are multiple external sources of environmental stress acting on the nature reserve. These include the neighbouring industrial harbour of Ravenna (Lucialli et al. 2007) as well as a surrounding landscape dominated by intense agriculture (Benini and Pezzi 2011). The heavy use of pesticides in Ravenna's

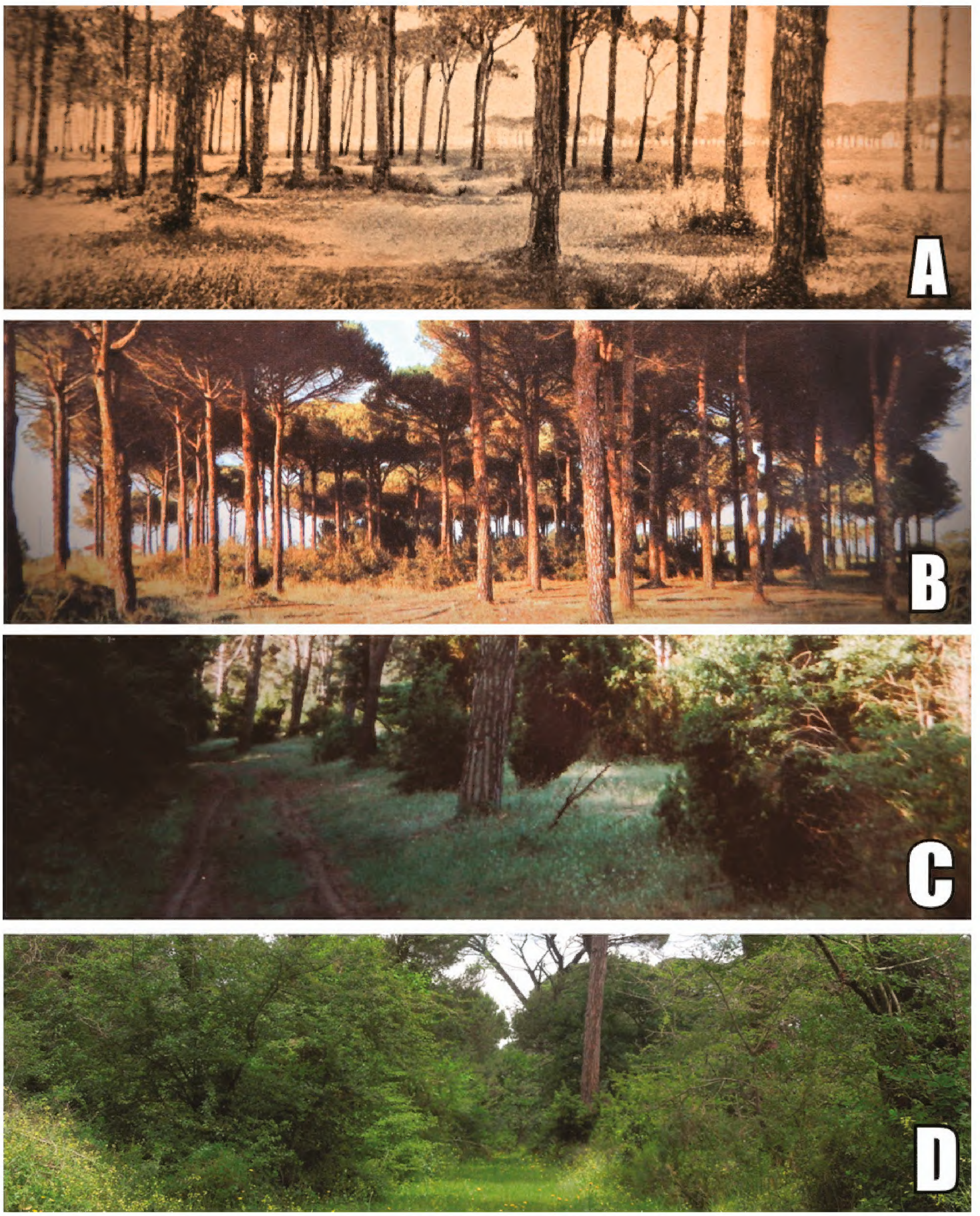

Figure 1. Succession of vegetation in PsV. **A** 1910 **B** 1970 **C** 1996 **D** 2017.

agriculture is also well documented (Paris et al. 2016). Therefore, pesticide drift must be considered to possibly affect organisms inside the reserve. Furthermore, the whole region is subject to subsidence induced soil salinisation, raising salt concentrations in soil water up to 22 g/l in PsV due to continual groundwater pumping and offshore gas production (Antonellini et al. 2008).

Finally, climate change is also evident in the region of Ravenna. Surface solar radiation in northern Italy decreased from 1959 until the mid-1980s, followed by an increase later on (Manara et al. 2016). Mean annual temperatures increased between 1961 and 2010 (Antolini et al. 2015), accompanied by substantial changes in precipitation levels. As a consequence, the overall aridity in the region has increased, particularly near the coastline (Appiotti et al. 2013).

Against this background, it is expected that – apart from mere stochastic effects on local colonisation and extinction promoted through isolation (Haddad et al. 2015) – natural succession, air pollution, soil salinisation, pesticide drift and climate change may have triggered long-term directional ecosystem changes in PsV.

We here combine multi-annual data from our own observations with a rare set of historical records to assess the transformation of the insect fauna in a Mediterranean coastal pine forest over the last 85 years. Regional lepidopterists visited PsV over many decades to conduct light-trapping, thereby collating faunal data for the area. We consider macromoths as suitable focal organisms for this type of study since they occur in high numbers, are rich in species and have short generation times (usually one year or less), rendering quick responses to environmental change visible. Moreover, moth species span a wide range of trophic affiliations, especially during their larval stages. Many species are quite specialised to particular host plants or habitat structures, which renders them susceptible to anthropogenic habitat changes (Fox 2013). With these data, we test the following hypotheses:

1. Species richness has overall decreased because of manifold anthropogenic influences and stochastic extinctions;
2. Species numbers of forest-bound moths have increased and non-forest moths decreased, due to the succession towards more forest cover within the reserve.

Material and methods

Historical moth data

To analyse multi-decadal changes in moth assemblages, data spanning a period of about 80 years were collated (Table 1). Two historical collections of moth specimens, accompanied by reliable data on sampling localities and sampling dates, were traced in regional natural history museums in Italy, viz. the Museo di Storia Naturale di Venezia (vouchers from 1933–1968) and the Museo Civico delle Cappuccine, Bagnacavallo (vouchers collected between 1966–1976). Further data were made available by a private collector, providing samples from the years 1977–1996 (E. Bertaccini, pers. communication). All moths, reliably labelled to have been collected in PsV, were considered for analysis. Identifications were cross-checked and corrected according to up-to-date taxonomy, whenever required. These historical voucher collections were qualitative in the sense that we have no information as to the reasons why collectors decided to keep or discard observed specimens. For sure, no large voucher series of

common species were assembled at these earlier times. We consider it likely that early collectors always kept vouchers of species that appeared to be 'new' to them for the site, whereas they may have ignored common species after their first observations.

Extant moth data

Data on the extant moth assemblages in PsV (expansion from north 44°31'39.15"N, 12°14'19.82"E to south 44°27'48.09"N, 12°13'43.67"E and west 44°29'51.96"N, 12°13'22.79"E to east 44°29'50.50"N, 12°14'15.56"E) were sampled by means of light-trapping in two time periods between 1997 and 2012, but in different manners. From 1997 to 2002, moths were attracted to one single light trap and manually sampled, mainly in early summer and early autumn, at seven locations within different types of vegetation (viz. downy oak forest, hygrophilous forest and, occasionally, reed or remaining open habitats). In the years 2011 and 2012, we more systematically collected moths in spring, early summer, high summer and autumn. This was done in four different habitat types prevalent in PsV (viz. reed, hygrophilous forest, downy oak forest and open habitats) to cover the moth community of the entire reserve as completely as possible. In 2011, automated light-traps were run at 20 sites rather equally distributed within PsV, which allowed sampling multiple habitats simultaneously. In 2012, the light trap employed from 1997 to 2002 was used again at nine locations. Moths were manually collected at this trap, but due to the high demand of manpower, this could be realised only at a smaller number of sites (see Table 1 for further details). All vouchers, sampled since 1997, are stored in the private collection of Mirko Wölfling (Niederwerrn, Germany).

Data management and analysis

Our primary target group were species of the monophyletic clade Macroheterocera sensu Regier et al. (2017), augmented by a handful of larger-sized representatives of Cossidae and Limacodidae that have traditionally been treated as 'macro-moths' by earlier European lepidopterists. Since our extant data were exclusively derived through light-trapping, we removed all strictly diurnally active Macroheterocera from the historical data to improve comparability. We also omitted species from the historical records that are on the wing only during the cold seasons, since we have no recent data for these parts of the year. Finally, we took out from all time periods species that only show up in NE Italy as sporadic or seasonal long-distance migrants, but which are not able to build up persistent populations there.

In a couple of cases, cryptic species diversity has been uncovered amongst moths represented in our data in recent years, while in the historical collections, these were still treated as just one species each. We then adopted the older (more inclusive) taxonomic species delineations for our analyses, since it was not possible to re-examine all historical records by means of anatomical or DNA-sequence based methods.

Table 1. Overview of the moth collections from PsV, available for evaluation. Only those moth species which qualified for a comparative analysis are considered in this tabulation (see Methods section).

Collection	Period	Number of recorded species	Number of trap locations	Type of trap and lamps
Callegari + Martinasco combined	1933–1976	107	Unknown	Unknown
Bertaccini	1977–1996	157	Unknown	Unknown
Wölfling Early extant data	1997–2002	174	7	500 W HWL, manual
Wölfling Recent extant data	2011–2012	187	20 (2011); 9 (2012)	2011: Sylvania 15 W BL + 15 W white BL, automated 2012: 500 W HWL, manual

For analysis, we partitioned our data into four time horizons. The first time horizon covered collections from 1933–1976 (collections Callegari and Martinasco), the second one refers to the period 1977–1996 (collection Bertaccini). The third time horizon was represented by our own samples from 1997–2002 and the fourth group by our own samples collected in 2011 and 2012.

For sample-based species richness estimation, each of the four time horizons had to be subdivided into sampling units. Since we have no information about the details of moth sampling in the old collections, we instead used individual calendar years as proxy for sampling units. This way, the moth data of the first time horizon were allocated to 33 subsamples and those of the second time horizon to 20 subsamples.

For the time horizon from 1997–2002, we instead used sampling nights as units. The same was done for the year 2012. In 2011, when automated light traps were used, we decided to choose sampled habitats per season rather than sampling nights. As the four automated light traps sampled four different habitats in one sampling night, choosing sampling nights as a unit would mean pooling data from different vegetation types. With manual light trapping, as it was performed in all the other years of our own sampling, just one vegetation type per night could be sampled. To adjust automated to manual samples by number of sampling units, choosing sampled habitats rather than sampling nights therefore seemed to be the most logical approach. As a consequence, we came up with 30 subsamples for the 1997–2002 timespan and 41 subsamples for the most recent timespan 2011/12.

For comparisons of moth species richness between the four temporal layers, we then analysed species accumulation by incidence data using the programme iNEXT online (Chao et al. 2016).

We further partitioned observed moth species into inhabitants of wooded habitats, species of open habitats, reed habitats and habitat generalist species, respectively. In three of these subsets, we again checked for temporal changes in species richness by means of species accumulation analysis across the four temporal layers, as described above. Reed species were too few to allow for a meaningful analysis through species accumulation statistics.

Finally, we used the information of species incidence counts to calculate the proportions of these for classes of habitat affiliations across the four time horizons. Using

χ^2-tests, we checked for significant differences in the representation of species per category of habitat use over the four time horizons. With these data, we also created pie charts to visualise the relationships between the different habitat users and how these might have changed proportionally over time.

Information about habitat affiliations of moth species was compiled from Ebert (1994–2003), Hausmann and Viidalepp (2012), Redondo et al. (2009), Rákosy (1996) and from various internet sources (www.lepiforum.de; www.pyrgus.de; www.euroleps.ch). The resulting classification of moth species into the four groups of habitat use can be found in Suppl. material 1: Table S1.

Results

In total, we assembled records of 403 macro-moth species for PsV. From these species, 103 species recorded in older collections had to be deleted from the analyses presented below, as they are either on the wing during the cold seasons only, show exclusively diurnal flight activity or only reach the area as sporadic long-distance migrants, leaving exactly 300 species of macro-moths for the present analyses. With the above adjustments, historical records could be traced for 219 macro-moth species that were observed in PsV during the 20th century. The two sets of historical collections comprised 107 (1933–1976: Callegari + Martinasco) and 157 species, respectively (1977–1996: Bertaccini). Our own samples covered in total 174 species from 1997–2002 and 187 species in the years 2011+2012 (237 species in total since 1997).

Altogether, 63 of the 219 species covered by historical records (28.8%) have never been observed again by us in PsV since 1997. We consider these below as 'lost' species. On the other hand, our data comprise records of 81 species that were not represented in the earlier collections ('gained' species). These gross figures indicate a substantial turnover in moth species composition over time, but they need to be controlled for sampling intensity prior to interpretation.

An incidence-based comparison of older time layers with the more recent datasets clearly shows a substantial increase in total macro-moth species richness after correcting for sampling intensity (Fig. 2). When extrapolated to a standardised number of 40 sample units, an estimated plus of about 67 species has occurred. In particular, 119 macro-moth species (± 13) were estimated for the oldest data, 193 species (± 21) for the time period from 1977–1996, 190 species (± 14) for the years 1997–2002 and 186 species (± 10) for the newest data. This corresponds to an increase by 56.3–59.7% in total moth species richness over the course of the entire time span, whereas almost no change is apparent if only the more recent data from the Bertaccini collection are taken as the basis.

Concerning the three classes of moth species according to their habitat use (Fig. 2), our comparisons at a standardised number of 40 samples revealed the following results. In total, 75 generalist species were observed over the last 80 years. From the oldest to the most recent time horizon, habitat generalists showed a plus of 28 species (1933–1976: 24 ± 6, 1977–1996: 56 ± 12, 1997–2002: 51 ± 4, 2011+2012: 52 ± 7), viz. an increase

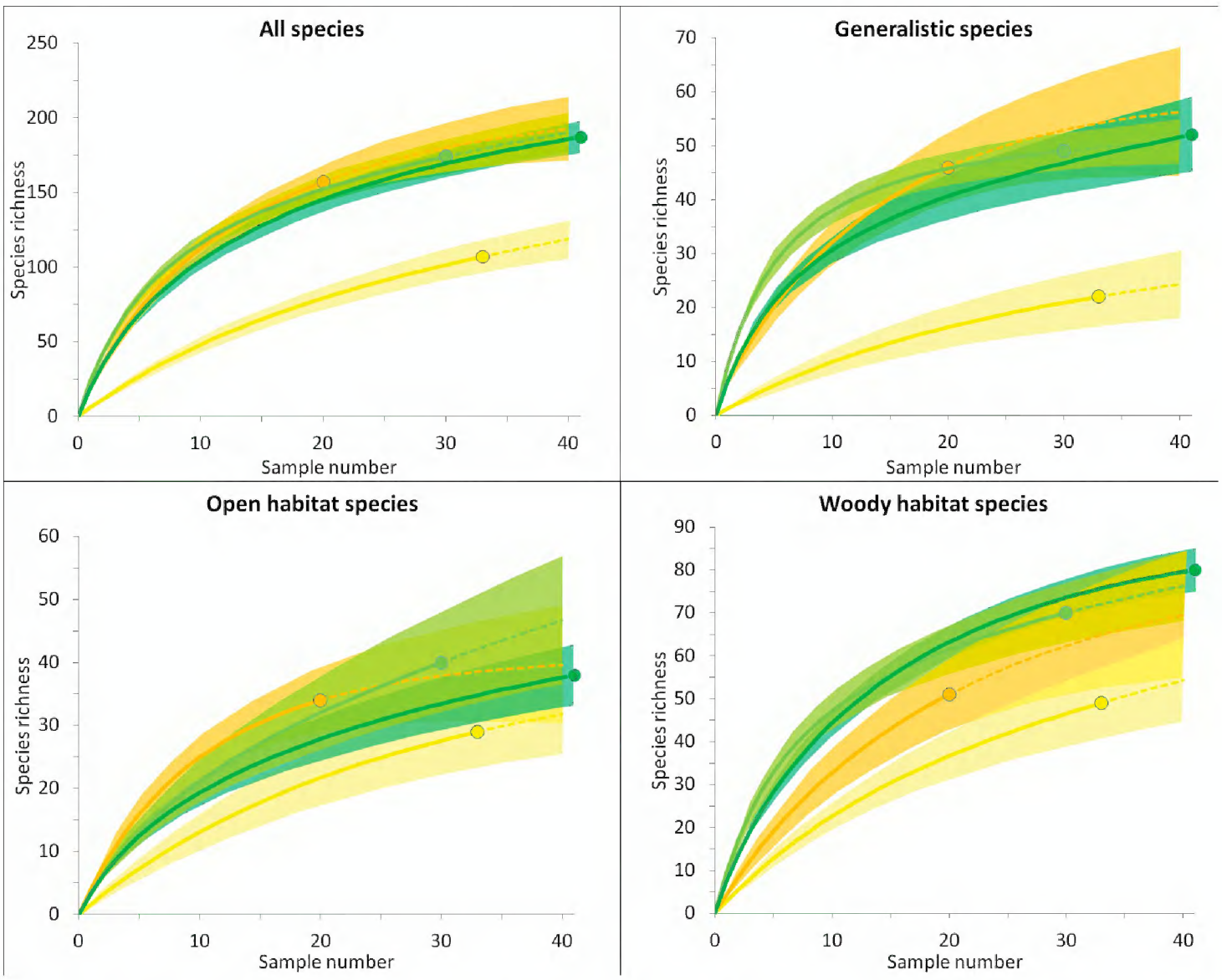

Figure 2. Species richness accumulation of macro-moths in PsV according to their habitat use, across four time horizons, as a function of the number of sampling units calculated in iNEXT. Shaded areas: 95% confidence limits. Yellow = 1933–1976, orange = 1977–1996, light green = 1997–2002, dark green = 2011/2012. Filled circles indicate observed species numbers at the respective number of available sampling units.

by 112.5–116.7%. Altogether, 123 woodland moth species were represented in the records. Woodland moths showed an estimated plus of 26 species over the full timespan (1933–1976: 54 ± 10, 1977–1996: 70 ± 14, 1997–2002: 76 ± 9, 2011+2012: 80 ± 5), which means an increase by 40.7–48.1%.

Overall, 73 open habitat species have thus far ever been recorded from PsV. With an estimated plus of 6 species, which refers to an 18.8–46.9% increase, open habitat users had the lowest increase in species numbers (1933–1976: 32 ± 7, 1977–1996: 40 ± 9, 1997–2002: 47 ± 10, 2011+2012: 38 ± 5). Observed species counts and the respective estimates for a standardised number of 40 sample units of macro-moths at the four time horizons in PsV, including segregation into classes of their habitat use, are listed in Table 2.

The contribution of moth species associated with individual habitat types (Fig. 3) revealed an increase in the proportion of generalist species, from 20.5% in the earliest samples to 32.3–37.4% around the year 2000 and later on. In contrast, the proportion of woodland species slightly decreased from 48.2% to 40.5%. Similarly, moth species

Table 2. Species counts and species richness estimates of macro-moths in PsV, segregated according to temporal layers and habitat use.

Habitat use	Old data	1970s	1997–2002	2011 & 2012
All species observed	107	157	174	187
Estimated species total	119	193	190	186
Generalist species observed	22	46	49	52
Generalist species estimated	24	56	51	52
Woodland species observed	49	51	71	81
Woodland species estimated	54	70	76	80
Open habitat species observed	29	34	40	38
Open habitat species estimated	32	40	47	38
Reed species observed	7	26	14	16
Reed species estimated	–	–	–	–

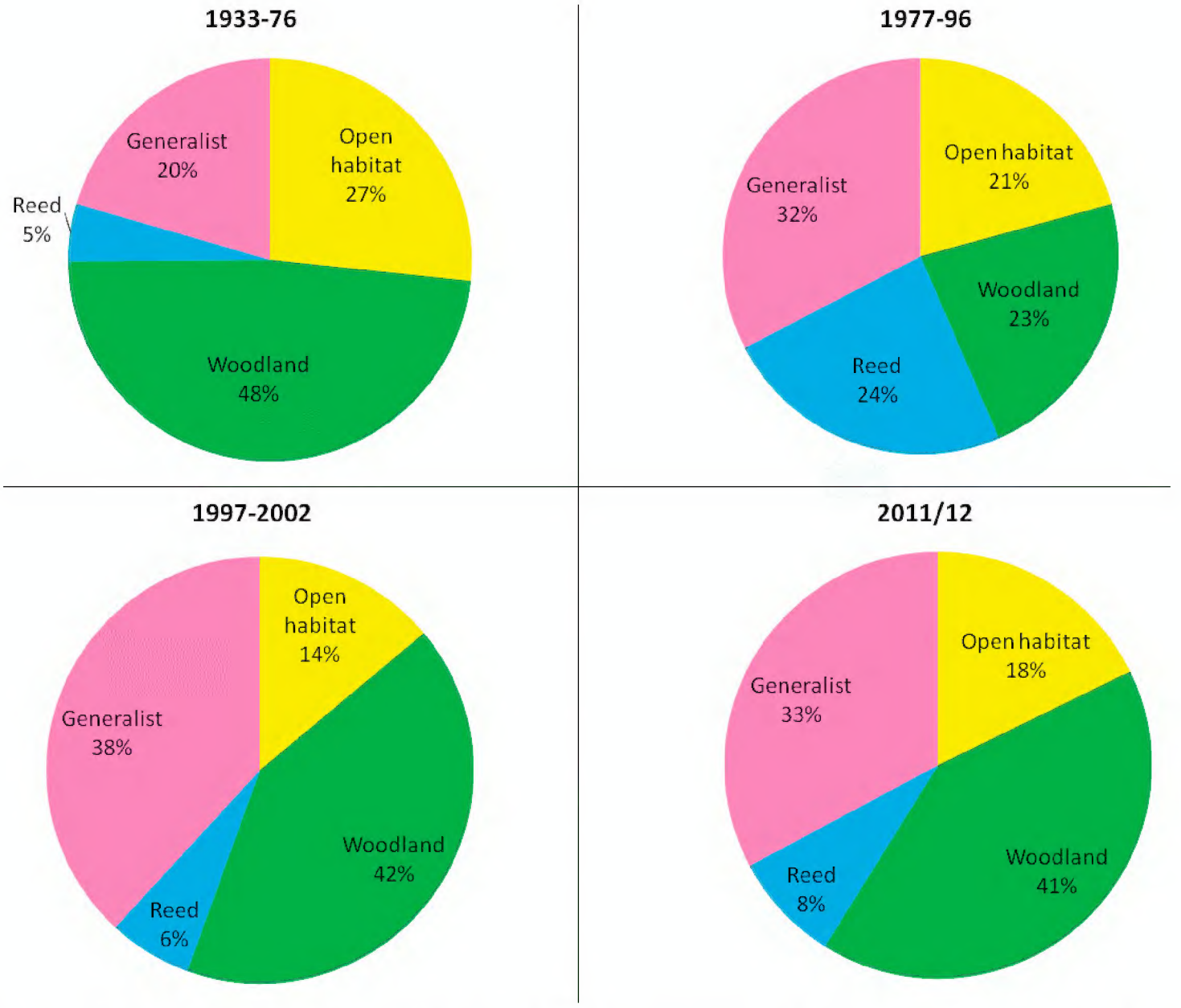

Figure 3. Proportions of macro-moth species in four classes according to habitat use, in the four time horizons.

of open habitats decreased in relative prevalence from 26.7% down to 13.6–17.5% of observed species. Reed species contributed only a minor fraction of 4.6–9.7% of the observed species richness per time horizon, except for the decades spanned by the

Table 3. Numbers of moth species no longer observed after 1995 in the reserve Pineta san Vitale ('lost'), only observed after 1997 ('gained') and present in historical as well as recent surveys ('persistent'), according to their major habitat affiliations.

Habitat use	Lost	Persistent	Gained
Open habitats	18	35	20
Woodland	25	57	41
Generalist	10	46	19
Reed	10	18	1

Bertaccini collection, when almost one quarter of the observed macro-moth species were reed dwellers. However, these differences of species numbers in the different types of habitat affiliations and time periods were just not significant (χ^2_{9df}=16.73, p=0.055).

A comparison of the number of species which disappeared during the last 80 years with those that were newly recorded since the mid-1990s revealed a substantial turnover in all four classes of moths according to their habitat use (Table 3). Amongst woodland species and habitat generalists, gains were almost twice as large as losses. In contrast, moth species of open or reed habitats were disproportionally prone to losses. These differences were statistically significant (χ^2_{6df}=15.78, p=0.015).

Discussion

Our study revealed that (1) contrary to expectation, total species richness of macro-moths did not decline obviously over the past 85 years; yet (2) indeed a substantial species turnover has occurred, favouring generalist and, to some extent, woodland species, while macro-moths of dry open grassland became far less prevalent than before and also reed species suffered from losses. The first observation is surprising, given the numerous stressors that act heavily on the isolated nature reserve PsV from its immediate surroundings. Observations in German nature reserves, embedded in landscapes of intensive agriculture, indicated that insect biomass has undergone severe reductions in the last decades (Hallmann et al. 2017). The same trend should be expected for PsV.

Apart from pressures exerted by the surrounding land-use, a severe extinction debt in isolated nature reserves such as PsV should be expected from demographic and environmental stochasticity alone (Bommarco et al. 2014). Hence, one might have anticipated a strong erosion of species richness over time (Halley et al. 2016). On the contrary, overall species richness of macro-moths appears to have increased over time, either when considered at a standardised sampling intensity or using the raw species counts. This richness pattern was also largely consistent across all groups of moths according to their habitat affiliations, though this apparent increase was strongest when all moths or only generalist species were considered.

We attribute this apparent, unexpected increase in moth species richness to two complementary reasons, viz. secondary succession and sampling intensity. After the definitive abandonment of land-use following the implementation of the current con-

servation status of PsV, succession has changed the vegetation of the area towards a more complex suite of woodland habitats, at the expense of dry open grassland (Fig. 1). Similar vegetation developments have also been observed elsewhere in northern Italy (Prisco et al. 2016). An increase in species richness should therefore be expected, since the number of niches available in an area usually increases with succession (Hilmers et al. 2018). Indeed, species accumulation analysis suggests that the number of woodland species steadily increased in PsV from the 1930s to the end of the 20th century, but has subsequently remained on the same high level over the past 20 years.

In this context, the species thriving in open and often xeric habitats are also informative. Richness of this group of species has increased the least and even decreased in the most recent collections, although our own quantitative light-trap samples were much larger and thus more comprehensive than earlier records available from PsV. Specifically, our own collections from the years 1997–2002 comprised 1655 moth individuals and those from 2011 and 2012 even 3192 individuals, as opposed to the Bertaccini collection (1459 specimens) and the oldest data (454 specimens). Hence, despite a higher likelihood of detecting open habitat species in these much larger samples, their contribution was low in our data. This well matches the fact that open xeric habitats have shrunk considerably in PsV over the last decades.

Moth species of reed habitats contributed only a minor fraction to the moth fauna of PsV, even though this particular nature reserve is part of a wetland national park of international relevance (Montanari 2010, Ramsar Convention Secretariat 2013). This habitat-specialist group of insects, like open habitat species, appears to have experienced disproportional biodiversity losses in recent decades. Despite the much larger size of our own moth samples, only one single additional reed species could be detected, whereas 10 moth species of reed habitats, present in old collections, have never been observed since 1997. However, our sampling efforts were not specifically targeted to surveying wetland species, so this might also be an effect of preferred sample locations of old collectors, for which we do not have concrete information.

In contrast, generalist species have increased in absolute species numbers, as well as in their relative contribution to the local fauna. This might indicate that generalists are better able to colonise isolated semi-natural areas than some specialised groups (Slade et al. 2013).

Apart from the overall increase in woodland, open and generalist species richness, which might be due to succession and increased sampling effort, the change in the proportions of the groups over time indicates that PsV, as an isolated nature reserve, might today favour the colonisation by generalist species and therefore fail in conserving specialised species (Rossetti et al. 2017). In fact, the proportion of generalists compared to the whole community increased most. These trends are in line with the notion that increasing human pressure on habitats favours generalists over specialists, thereby contributing to biotic homogenisation (Mangels et al. 2017).

Apart from true species turnover, the apparent increase in species richness may partially be due to the way in which historical collections have been assembled. We do not know which kind of light trap was used by early lepidopterists, but in the 1930s, collectors did not have access to lamps powered by electricity with substantial

light emission in the near-UV range. They instead often used petrol lanterns with lower efficiency in attracting nocturnal insects. Moreover, lepidopterists with a keen interest in faunistic research tended to be biased towards keeping records preferentially of the 'more interesting' species, i.e. those that are regionally rare or otherwise charismatic. In hindsight, it is impossible to safely tell which species, lacking in old collections, are 'false negatives' (i.e. species that were present, but went unnoticed or no vouchers were kept). However, a number of conspicuous species like *Hemithea aestivaria*, *Opisthograptis luteolata* and *Lacanobia w-latinum*, which collectors of the old data would surely have taken, only appeared in the new data. In contrast, small and 'uncharismatic' species like *Idaea straminata* and *Deltote pygarga* were sampled by old collectors. In order to compensate for differences in sampling effort, we allocated the old data into two time horizons yielding subsets of roughly similar size. We consider comparing two 'historical' periods of low effort sampling with six years of medium and two years of high sampling effort, suitable to facilitate comparisons. We acknowledge that analysis of data from non-standardised sampling by extrapolation is always prone to critique. However, even by comparing the raw data, old collections comprised fewer species than the newer ones (about 80 species). We therefore conclude that the lower richness of the older collections is not only due to sampling effects, but indeed reflects the appearance of new species in the reserve over time.

Even though our results might indicate that preservation of moth biodiversity works quite well within the reserve PsV, many moth species have apparently completely disappeared. We never observed 63 (out of 219) species recorded at least once between 1933 and 1996 during our own light-trapping campaigns. These lost species include conspicuous species (e.g. *Calophasia lunula*, *Plusia festucae*, *Diachrysia chryson* and *Sphinx ligustri*) that are very unlikely to have gone undetected by chance in the period between 1997 and 2012. Lost species also comprise a few species of high conservation concern (e.g. *Calyptra thalictri* and the very rare and localised wetland geometrid *Chariaspilates formosaria*). Even though one can never be entirely sure whether 'lost' species are really locally extinct or whether 'gained' species had not existed earlier in PsV, yet escaped discovery, our analyses show that species turnover in the reserve was non-random.

Overall, these considerations indicate that (a) a substantial extinction debt still remains a risk for the fauna of PsV: more local species extinctions are to be expected, just as the losses that have occurred in earlier decades; and that (b) the process of biotic homogenisation (Newbold et al. 2018) is likely to proceed here as well. Generalist species already play a larger role in faunal composition than was the case with the historical data. Similarly, moth communities across many regions in Europe tend to become ever more homogeneous, with generalist ubiquitous species replacing specialists (Mangels et al. 2017; Franzén and Betzholtz 2012).

Our analyses indicate that, apart from an apparent increase in recorded species numbers, this area of high legal conservation status is indeed threatened by further erosion of its biodiversity, mainly due to the risk of a strong extinction debt, as well as by landscape-level constraints on recolonisation once species have locally gone missing. In the long run, even though the vegetation in PsV may continue to converge to a more 'natural'

structure, the insect fauna in this highly isolated area might be prone to further homogenisation. Therefore, active conservation management is most desirable, for example with focus on wetland or open habitat fractions remaining as niches for specialist organisms, in order to safeguard the function of PsV in the context of preserving biodiversity.

Conclusions

To understand changes in insect diversity, there is a strong need for long term analyses. Yet, long-term data from standardised monitoring are largely lacking. Historical collections not only provide an opportunity to gain an insight into community change, but also pose challenges, such as selective or variable sampling effort and gaps in time series. We tried here to extract valuable information on the long term development of biota in an isolated nature reserve by analysing such old collections.

In contrast to our expectations, species richness increased although isolation effects, increased salinity and pesticide use in nearby agricultural areas might have affected the reserve. Therefore, succession might even override these negative effects and conceal possible influences on moth species richness. Open habitat specialists have been lost to a disproportionate extent, whereas generalist and woodland species have increased. These trends reflect both the succession inside the forest reserve, as well as constraints on species dispersal in fragmented landscapes. From a conservation perspective, enhancing connectivity between such reserves is of the highest importance for protecting specialised and rare species.

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Supplementary material 1

Table S1. Species of Pineta san Vitale splitted into different types of habitat use

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Data type: species data

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